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THE DEVELOPMENT OF THE SHELL IN THE COILED STAGE OF *BACULITES COMPRESSUS* SAY.

BY AMOS P. BROWN.

In a former brief communication¹ the writer has noted the discovery of the young of the above species in some Cretaceous marl from near Deadwood, S. Dak., and has shown that *Baculites* was coiled in its earlier stages. In the same communication the development of the suture is illustrated from a generalized *Ceratite* stage to the adult suture of *B. compressus*, thus fixing the species of these young forms. Since the above was communicated the writer has been engaged in the study of the development of the shell in the coiled stage and the results of these investigations are presented herewith.

The coiled stage of the shell consists of two to two and one-half whorls, the diameter of this coiled portion being 0.8 to 1. mm. The shell then passes at once into the straight form, either tangent to the spiral or somewhat reflexed in certain cases. By breaking the shell back from the straight portion to the protoconch, the development of the shell was made out and the successive stages in this development observed. By an examination of the surface markings of the shell the form and extent of the embryonic shell on leaving the egg—the first naëpionic stage—has been determined with considerable certainty.

The protoconch appears on a front view broadly elliptical in outline, being 0.55 mm. to 0.60 mm. in axial diameter by 0.45 mm. in vertical diameter; this axial diameter then diminishes in each succeeding whorl and is not again attained until a length of several millimeters of the straight portion of the shell has been developed. Hence the rounded ends of the protoconch may generally be seen projecting beyond the succeeding whorls when the entire spiral portion of the shell is viewed edgewise. The suture line of the first septum is marked by the prominent narrow saddle over the siphuncle which determines that this form belongs to the *Angustisellati* of Branco. The remainder of the first septum is rather simply curved, the lateral saddles of the succeeding septa being perhaps represented by the slight lateral undulations that exist. Seen from the side the protoconch has the form shown in Pl. IX, fig. 4, while

¹Proc. Acad. Nat. Sci., Phila., 1891, pp. 159-160.

the front view is shown in fig. 3. In this latter the form of the septum may be readily seen, and also the position of the siphuncle. It will be noticed that the perforation of the siphuncle is large (0.07 mm. in diameter), this diameter of the perforation remains quite constant throughout the spiral portion of the shell. The form of the first septum is lunate, 0.55 mm. broad by 0.15 mm. high and the lateral extremities reach to near the axis of the spiral. The next following septa have successively smaller lateral diameters and larger vertical diameters, so that the successive whorls become rapidly less and less enveloping. The form of the septa at the same time is gradually changing; the lunate form of the first septum gives place to a broadly elliptical form concave on the inner side; this in turn passes into a more and more circular form, until it becomes completely circular in the straight portion of the shell. Thus Plate IX, fig. 8, shows the fourth septum to be 0.52 mm. broad by 0.21 mm. high, the total vertical diameter of the shell at this point being 0.56 mm. or about the same as the lateral. The seventh septum measures 0.47 mm. by 0.23 mm. high; the thirteenth, Plate IX, fig. 7, measures 0.45 mm. broad by 0.28 mm. high. Finally the seventeenth septum, Plate IX, fig. 6, measures 0.50 mm. broad by 0.40 mm. high, showing that the minimum breadth has been passed, and in fact at about the fourteenth septum the breadth seems to be least. It will be noticed that the surface of contact between the inner and outer whorls rapidly diminishes from 0.55 mm. at the first septum to 0.20 mm. at the seventeenth septum, and thence rapidly to the straight portion which begins somewhere between the twentieth and twenty-fifth septa. This surface of contact may be readily traced on the inner whorls of the shell and these traces are indicated in Plate IX, figs. 6, 7 and 8. In the straight portion of the shell the form of cross section passes gradually from a circular to an ovoidal, laterally compressed form and finally in the adult into a somewhat triangular form, acute ventrally (the side on which the siphuncle is located) and flattened dorsally. The cross section of the shell is thus seen to be first lunate, laterally elongated; then successively laterally elliptical, circular, laterally compressed, and finally somewhat triangular. These changes up to the circular form take place very rapidly; the succeeding changes from the circular form to the triangular form are very gradual. In this respect the shell shows very rapid development in the spiral stage and gradual development on quite new lines in the

straight stage. It is also to be noted in this connection that some other species of *Baculites*, as *B. ovatus* Say, *B. anceps* Lam., have a circular or ovate cross section in the adult stage, and probably pass through the same changes as the species under discussion in their earlier stages up to the circular cross section but retain this circular or ovate cross section in the adult.

An examination of the suture lines as represented in Pl. IX, fig. 9, will show quite rapid development here too, but probably not more than is common to all of the Ammonitidæ. As is usual the form of the second suture is entirely different from that of the first. The ventral lobe in the second suture is well marked, the first lateral saddle is here quite broad, the first lateral lobe is acute, and a portion of the second lateral saddle is shown. The ventral lobe of the third suture is a straight line on the end; in the fourth the narrow ventral saddle, which is located over the siphuncle, first appears. The lateral lobes of the third suture are rounded instead of acute as in the second suture and in each succeeding suture the lobes and saddles become more rounded and deeper until they are deeper than broad. During this period of its development the shell may be said to be in the Goniatic stage which persists throughout the spiral shell and as far as about the 30th septum, when the secondary lobes begin to appear at the ends of the lateral saddles and the shell passes into what might be called the Ceratitic stage. This Ceratitic stage then rapidly gives place to the typical Ammonite stage in which both the lateral lobes and saddles become divided at their ends. Pl. IX, fig. 9, illustrates the development of the suture from the initial to the Goniatic stage. Its development in the Ceratitic and Ammonite stages has been illustrated in my former communication on this species already referred to above. The completion of the second lateral lobe and dorsal saddle has probably already taken place on the surface of contact between the protoconch and the first whorl as early as the second suture, though it does not appear on the free surface until the sixth suture has been reached. Owing to the difficulty of handling these exceedingly minute and friable pieces of the shell broken off in displaying the inner whorls and the protoconch no attempt has been made to observe the form of suture on this surface of contact between the inner and outer whorls, but from examining the front view of the septa as they were successively exposed, it was found that the main features of the lobes and saddles first develop on this surface of con-

tact and then appear from the inner side of the whorl on the free outer surface, being exposed by the uncoiling of the shell. The total number of main lobes and saddles of the adult shell is apparently developed at the second septum, and the further development of the suture consists in the formation of secondary lobes and saddles, appearing as complexities of the primary or main ones. Of these secondary folds of the suture, the first to appear is the narrow ventral saddle at the fourth suture, and probably also the narrow dorsal lobe is formed but little later, for both are about equally well marked when the shell passes into the straight form. The fact that the adult number of lobes is developed at the second septum is an evidence of cataplastic development, the adult number of lobes in the suture being usually developed at a much later stage in the normal coiled *Ammonites*. But in other uncoiled and degenerate forms the naepionic lobes are retained throughout their development and are not added to in the adult stages.

The outer nacreous shell when preserved is found to be marked by minute tuberculations of irregular shape; these in turn give place to the parallel curved lines seen in the adult shell. These parallel lines first appear about the fourteenth septum, and they soon completely obscure the tuberculation. Between the first and second sutures there is apparently an interruption in the growth of the shell, appearing as a line resembling a suture line, Pl. IX, fig. 10. This line seems to be slightly raised above the general shell substance; it extends over the end of the ventral lobe of the second suture and back in a simple curve to near the lateral ends of the first suture. In breaking away the nacreous shell substance to show the sutures, the break nearly always follows this line, leaving the protoconch covered by the original shell. Over the area thus left of the original shell substance the tuberculations are found to be more circular in outline and closer together than in the succeeding portions of the shell. It is believed that the portion of the shell thus bounded represents the original embryonic chamber, or protoconch Pl. IX, fig. 5, which would thus extend beyond the point where the first septum was subsequently developed. A section in the plane of the spiral, but not quite median, Pl. IX, fig. 11, showed the shell to be composed of successively deposited layers, and the first of these was seen to extend a short distance beyond the first septum, thus tending to confirm the above belief. It thus seems probable that the outer limit of the protoconch lies between the first and second

septa, as shown in Pl. IX, fig. 10. The edge of this supposed embryonic shell is seen to be finely crenate, but not regularly so, the crenatures being larger in some parts than in others. On breaking away the outer shell of the protoconch this line still persists and it might readily be mistaken for a suture line, if it did not overlap the lobe of the second suture. The section of the shell in the plane of the spiral above referred to shows that there is no septum at this point, but there is apparently a slight thickening of the shell substance.

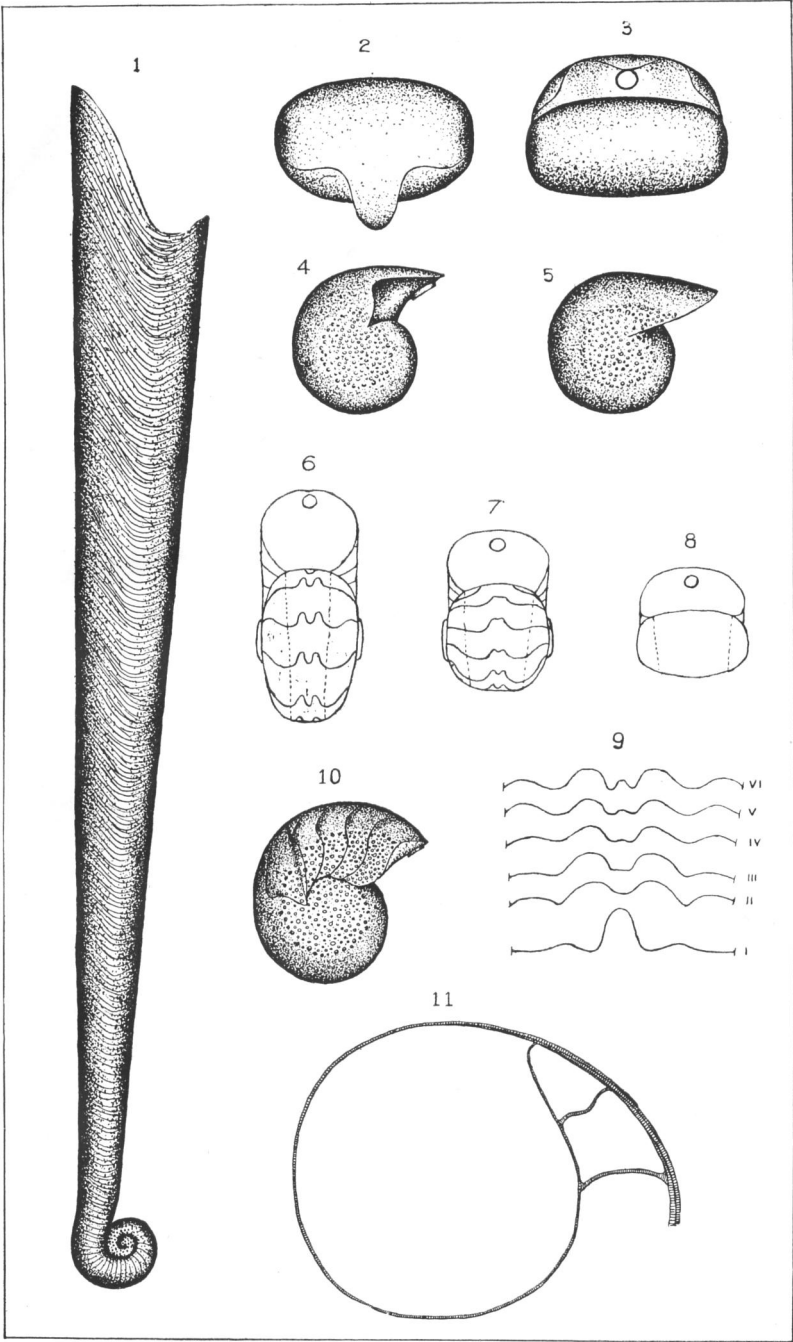
The protoconch, as seen in this section in the plane of the spiral, Pl. IX, fig. 11, is quite large and nearly circular, and of the general form common to all of the Ammonoidea. The section not being quite median the siphuncle is not shown, and the septa do not present exactly the same form as they would in a median section. Only one such section was ground on account of scarcity of material to work on, but this one shows the structure to be that of the Ammonoidea in general. The septa were equally spaced, or nearly so, up to the twelfth, from which point they are successively more widely spaced. It is to be noted that at about this point the lateral contraction of the shell ceases and the gradual increase in lateral diameter begins, apparently indicating a change in the conditions of the life of the animal.

After considerable investigation I have been unable as yet to trace the phylogeny of this species. A careful examination of the development of the shell in the earlier stages of *Scaphites conradi* Morton, a form associated with the young of *Baculites* in this same material, showed that the *Scaphites* must have been derived from a totally different stock, and cannot be related to *Baculites*. Nor do the adult suture lines of the two forms show much resemblance to each other. An interesting point was developed, however, in the study of the young of the *Scaphites*, which tends to confirm my observation on the extent of the first embryonic shell as shown in Pl. IX, fig. 5. A very successful median section of *Scaphites conradi* in the plane of the spiral showed a thickening of the shell at the termination of the first layer, which is between the first and second septa as in *Baculites*, this thickening indicating an interruption in the growth of the shell such as might be expected on the emerging of the young from the egg. But this correspondence in the extent of the embryonic shell does not indicate a relation between the two forms, it being a character probably common to all Ammonites. Indeed,

judging from the adult characters alone, this *Baculites* is much more closely related to the forms grouped under the genus *Ancyloceras*, and as far as the young of *Ancyloceras* has been described it seems to be closely related to *Baculites*. On comparing the adult sutures of *B. compressus* with *Ancyloceras jenneyi* Whitf., the similarity is very marked. Lack of suitable material has prevented my examining the young of *Ancyloceras*, but I would suggest that to the genera *Ancyloceras*, *Crioceras*, and related forms with completely separate whorls we are to look for the nearest relatives of *Baculites*. These forms, like *Baculites*, have become uncoiled at a very early stage; their adult sutures are very similar, and the main difference lies in the degree of straightening of the shell. Indeed in *Baculites* the shell is not strictly rectilinear but there is usually a slight curvature towards the dorsal side. While then the relations of this form are still in doubt, it is hoped that the facts presented in this paper may go far towards unravelling the phylogeny of *Baculites*.

EXPLANATION OF PLATE IX.

- Fig. 1. Young of *Baculites compressus* Say, x10.
- Fig. 2. Protoconch seen from above, x45.
- Fig. 3. Protoconch front view, x45.
- Fig. 4. Protoconch side view, x45.
- Fig. 5. Embryonic shell of first naëpionic stage, side view, x45. This is probably the shell possessed by the animal on leaving the egg.
- Fig. 6. Front view at the seventeenth septum, showing cross section of the whorl, x25. In this and the two succeeding figures the dotted lines indicate the extent of the surface of contact between this portion of the shell and the succeeding whorl.
- Fig. 7. Front view at thirteenth septum, x25.
- Fig. 8. Front view at fourth septum, x25.
- Fig. 9. The first six suture lines, x35.
- Fig. 10. Side view of protoconch and first six septa, showing outline of the first naëpionic stage, x40.
- Fig. 11. Cross section of shell in the plane of the spiral showing two septa and the imbricated layers of growth, x100.



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BROWN, SPIRE OF BACULITES.